

A RE-EXAMINATION OF THE CHESTNUT-SHOULDERED WREN COMPLEX OF AUSTRALIA

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SYNOPSIS

THE chestnut-shouldered wren complex within the genus *Malurus* is re-examined, using recently collected material. Seven forms are recognized—*elegans*, *pulcherrimus*, *lamberti*, *assimilis* (including *mastersi* and *bernieri*), *rogersi*, *dulcis* and *amabilis*. Variations occur within *assimilis*, *rogersi* and *amabilis*. Some variant individuals from the northern edge of the range of *assimilis* show aspects of plumage colour approaching those of other nearby forms. The type of distribution appears to provide an example of the refuge concept suggested by Keast. It is suggested that *pulcherrimus* originated in the Eyre peninsula region and *assimilis* in the Hamersley region, and that adaptation to warmer and drier conditions enabled these forms to spread with subsequent climatic amelioration. A wide tolerance of habitat is shown by *assimilis*. Other forms appear to have more specific preferences but may be occupying the ecological equivalent, within their range, of the general habitat required. Evidence of interaction and difference between forms indicates that *elegans* and *pulcherrimus* behave as good species.

The taxonomic status of the other five forms appears to be equal, but whether this should be specific or subspecific must remain undecided until there is more information on distribution and possible interbreeding.

Certain broad trends in plumage colour and size are apparent. The blue wrens appear to have originated as forest birds, probably in the New Guinea region, and to have evolved dull female and male eclipse plumages for crypsis. It is suggested that the dull plumage on the crowns of breeding males of *assimilis* may represent a similar trend.

INTRODUCTION

When the accumulated specimens of blue wrens, *Malurus* species, collected during the five phases of the Harold Hall Australian Expedition were examined for completion of the final report, a re-examination was made of the forms within the chestnut-shouldered wren complex. The last revision had been that of Mack (1934). Seven forms are recognized in the present study (Map 1), these having been assigned various taxonomic ranks during the past. In order to avoid any prior assumption of taxonomic status a single specific or subspecific name has been used in referring to each population in the following account. In addition to specimens collected on the expedition, material already in the collection of the British Museum (Natural History) and specimens borrowed from various Australian museums have been used.

COMMON CHARACTERS

All birds of both sexes have blue colouring, often rather dull, on the rectrices. Males in breeding plumage have a black rump, a broad black collar posterior to the ear-coverts and extending round the nape, and black lores. They also have scapular patches of rather long chestnut-red feathers, the depth of colour on these tending to vary with the intensity of the general plumage colour. The pale edges of the tertials are also tinted chestnut-red. When not breeding males moult into an

eclipse plumage similar to that of females and immature birds of both sexes. I have used the term "eclipse" plumage in preference to "non-breeding" plumage since in some species of *Malurus* apparently adult males in breeding condition have the plain plumage and are capable of breeding while in this plumage; thus while the bright male colouring is undoubtedly a breeding plumage the converse is not always true.

The plumage of females, immature birds, and eclipse males is plain brown or blue-grey, according to the form. In those forms in which females have chestnut-red on the lores and around the eyes, similar colour is present on immature birds of both sexes. In these forms adult males do not regain this chestnut-red colour on the lores after the first breeding plumage, although there may be some chestnut-red on a few feathers immediately around the eye.

In moulting into the full breeding plumage, males of *elegans* and *pulcherrimus* appear to acquire the full black lores while still otherwise in eclipse plumage, after which bright blue feathers appear first immediately around the eye. The former character was not apparent on a large series of specimens of *assimilis* and a few of *lamberti* and *rogersi*, save for one brown-plumaged male specimen of *assimilis* with completely black lores.

Except in *amabilis*, females and immature birds have reddish-brown bills. Males in breeding condition have black bills, but may show some brown on a dark bill



MAP 1. The ranges as indicated here are very tentative and should be regarded only as a generalized diagram for the purpose of discussing relationship. The question marks indicate regions where the ranges are in doubt, and within the areas shown populations might be small and scattered.

when in non-breeding plumage; while immature males approaching maturity show an increasing spread of black.

Certain broad tendencies are apparent over the chestnut-shouldered wren group as a whole. South-western birds tend to have purple breasts, north-eastern birds to have white lores, northern birds to have blue-grey females and eclipse males, and eastern birds to be bluer and less violet. Birds tend to become larger towards the northerly and southerly limits of distribution.

FORMS OF THE CHESTNUT-SHOULDERED WRENS

Seven forms are recognized here and the accompanying table shows the major differences in plumage between these. The forms are as follows.

	Lores of ♀	Plumage of ♀	Flank of ♂	Breast of ♂
<i>elegans</i>	chestnut-red	rufous-brown and greyish-brown	pale buff	blue-black
<i>pulcherrimus</i>	chestnut-red	olivaceous-brown	pale buff	dark violet
<i>lamberti</i>	chestnut-red	warm brown	pale buff	black
<i>assimilis</i>	chestnut-red	light brown	pale buff	black
<i>rogersi</i>	chestnut-red	light blue-grey	white or greyish	black
<i>dulcis</i>	white	light blue-grey	white or greyish	black
<i>amabilis</i>	white	dark blue	very pale buff	black

1. *elegans*. The Red-winged Wren.

This is restricted in distribution to the extreme south-west of Western Australia, where it is found in thick cover associated with swamps, streams and lakes in areas between Gingin and Warriup.

The male is the palest of these forms, being medium blue on crown and nape, gradually changing on the sides of the head to very pale azure blue: paler still on the ear-coverts where it has been described as "silvery". The back is an even paler and more azure tint. The breast is blackish but with a strong violet tint producing a blue-black colour; the latter most apparent when the bird is viewed frontally with the bill raised and light falling directly on the underside, the breast appearing deep violet with a black band along its lower edge. The hind-flanks and under tail coverts are tinted with pale buff. The female is dark greyish-brown on the head, and dark rufous-brown on the back and wings. Below it is light greyish-buff on throat and breast and pale buff on belly and flanks. The lores are deep chestnut-red.

2. *pulcherrimus*. The Blue-breasted Wren.

This form appears in a zone north of that of *elegans* and mostly south of that of *assimilis*. Its western limits are between the mouths of the Murchison and Namban Rivers and its range extends through the mallee and wheatbelt in a south-easterly zone to Warriup and Eucly, with an apparently isolate population on the Eyre Peninsula.

The male is a deep violaceous blue on the head and deep violet on the back. The forehead and sides of the head are more blue, becoming light blue on the ear-coverts.

The breast is glossy dark violet, brighter towards the edges of the sides, and with a narrow black band along its lower edge. The flanks and under tail coverts are a drab light buff. The female is dull olivaceous brown, with chestnut-red lores. Below, the throat and breast are pale greyish-buff, the belly white, and the flanks and under tail coverts light buff.

3. *lamberti*. Usually regarded as the eastern form of the Variegated Wren, *assimilis*; but sometimes called Lambert's Wren.

This form occurs on the eastern seaboard, and the range appears to be the region east of the Great Dividing Range, south to Sydney and north at least to the Brisbane region, although there appears to be little evidence of what occurs near the coast north of this. Further inland, specimens collected by Elsey (Macdonald and Colston 1965) on the Belyando River are certainly *assimilis* and the latter is said to have been collected on the Dawson River (White 1916). These rivers, although inland in the complex topography of the Dividing Range in mid-Queensland, drain towards the east. Two female specimens collected at Bloomsbury, near Prosperine, on the Wilkins Expedition (allowing for foxing and comparing them with material taken elsewhere on the same expedition) are of the *lamberti* form, suggesting that the latter extends well up the east coast.

Males of this form are deep blue, but not violet-blue, on the back and nape; becoming paler blue on forehead, sides of head and ear-coverts, the last having, in comparison with other light blue plumage, a slight azure tint. There are violet tips to feathers bordering the sides of the black breast. Posterior flank feathers are pale buff. Females, immature birds and males in eclipse are brown above, tinted with warm buff on the rump; pale below with yellowish buff on flanks and belly; and have deep chestnut-red on the lores and a narrow ring round the eye. The brown colour on these birds is darker and warmer in tint than that of *assimilis*.

4. *assimilis*. The Variegated Wren.

This form appears to occur from the Great Dividing Range and its ancillary ranges in Queensland, westwards across the entire dry central region to the west coast, north to the Gulf of Carpentaria, the Roper River, and the Broome Area of Western Australia, and south to the edges of the range of *pulcherrimus* but apparently not as far as the south coast.

Males are violet-blue on the back, nape and crown, grading into deep blue on the forehead and light blue, often slightly azure, on ear-coverts and around the eye. Some individuals are less violet dorsally, lighter blue on the head, and more azure on the ear-coverts. The posterior flanks are pale buff. There are violet tips to feathers bordering the sides of the black breast. Of 33 adult males apparently in full breeding plumage and not moulting, 17 showed an area of dull brownish colour on the crown on the head, often resembling a distinct but irregular cap. Another five show traces of this and only 11 have fully-coloured heads. Females, immature birds and males in eclipse are a dull, light brown above, with a buffish rump. Below they are pale buff, deepest on the flanks and almost absent from the throat. Adult males in this plumage, in addition to lacking the chestnut-red lores present on the others, are much whiter below.

5. *rogersi*. Usually regarded as the Western form of the Dulcet or Lavender-flanked Wren, *dulcis*.

From specimens collected, and from others kindly lent by the Western Australian Museum, this form occurs in the ranges of the Kimberleys from the Leopold Range north to Napier Broome Bay and westward to the Ord River.

Dorsally males of this form are virtually indistinguishable from those of *assimilis*, but do not show the extreme violaceous tint of some individuals of the latter and tend to come about the middle of the range of variation of the blue and violet colours. There is some individual variation. The wing feathers, both flights and coverts, are a darker brown than those of *assimilis* and may show a faint bluish sheen. This is apparent in fresh plumage, but an otherwise moulted male specimen showed old wing feathers of a similar, sandier brown colour to those of *assimilis*, with just a few darker new feathers. There are violet tips to feathers bordering the breast. The belly and flanks are white, and of ten specimens only one shows a faint greyish wash with even fainter violet tint which might have given rise to the vernacular name. In the circumstances it would seem more correct to call this species "White-flanked" rather than "Lavender-flanked" if it is desirable to refer to this aspect of the plumage.

Females, immatures and males in eclipse plumage all have a dorsal plumage of dull blue-grey, becoming paler blue on the sides of the head and neck. Males are more blue and less grey, and very young birds are greyer, with a hint of brown, and less blue. Wing-coverts are dark brown with greyish edges. Both females and immature males show the chestnut-red lores that substantiate Mathew's *rogersi*. Females show a very pale buff tint on the underside, while males in eclipse plumage are almost white below.

6. *dulcis*. The typical Dulcet or White-flanked Wren.

This form is usually said to have a rather restricted distribution between the Mary and King Rivers (the northern King River), in Northern Territory; (Storr 1967). Humphries (1947) refers to *M. amabilis* [= *dulcis*] being observed on one occasion at Melville Bay, and more recently Rix (1970) has recorded this species at Elsey Creek on the upper Roper River. It therefore seems possible that its true range may be around, or through, the Arnhem Land Region.

Males appear almost indistinguishable from *rogersi* but in fresh plumage appear to show a more obvious bluish wash on the wing feathers, particularly the coverts, making these appear darker in colour. Females and immature males differ from *rogersi* in being slightly darker dorsally, but more conspicuously in having the lores and a narrow ring round the eye creamy-white and not chestnut-red. Ventrally the very pale buff colour is apparent but is combined with a faint grey tint to give the plumage of the underside a rather drab appearance.

7. *amabilis*. The Lovely Wren.

This is another form with apparently limited distribution, occupying habitats bordering the rainforest along the north-east Queensland coast between Cape York and Cardwell, but it has also been recorded (Thompson 1935) from the Gulf coastal

regions on the Lower Edward River where it was noted and collected in "dense dry scrubby country on raised beaches".

Males are most similar to *lamberti*, but are a lighter, clearer blue on the back and head, without any definite violet or azure tints, the ear-coverts being similar in colour to the rest of the head. The violet tips to feathers at the sides of the breast are restricted to a few vestigial tips. The flanks show some pale buff. The pale edges to wing feathers show a more distinct blue wash, and these feathers are otherwise very dark in colour, in some instances practically black, and in the case of the lesser coverts usually black.

Females, immature males and males in eclipse resemble those of *dulcis* in having creamy-white lores and eye-rims, but differ in the much darker colour of the dorsal plumage. The latter is a dark and rather dull blue, becoming a little lighter on the forehead, and with conspicuous light blue ear-coverts. Both females and males in eclipse show black bases to the feathers across the upper mantle which are wholly black in the breeding males. The bill is black in both sexes. Wing feathers are dark with a dark blue wash. Below the plumage is very pale buff, whiter on the throat, and whiter overall on males. The juvenile is browner and less blue on the back, and has a dark, blackish-brown bill.

VARIATION WITHIN FORMS

Individual variation is apparent within *assimilis*, *rogersi* and *amabilis*. It is *assimilis*, with its very extensive range, which shows the greatest variation. Individuals showing some variation were described as new races and originally nine were recognized within the range of this form, but these were reduced by Mack (1934) to three (Map 2). On the basis of the material examined, I cannot agree that there are three readily recognizable subspecies within this area, but there is some tendency toward broad trends in colour variation within the very large range occupied by this form.

As already mentioned, the only obvious difference is for some individuals to have paler heads. In comparing the blue colour it is necessary to have specimens side by side at the same angle to the light, since the incidence of light can affect the apparent hue of structural colours of feathers.

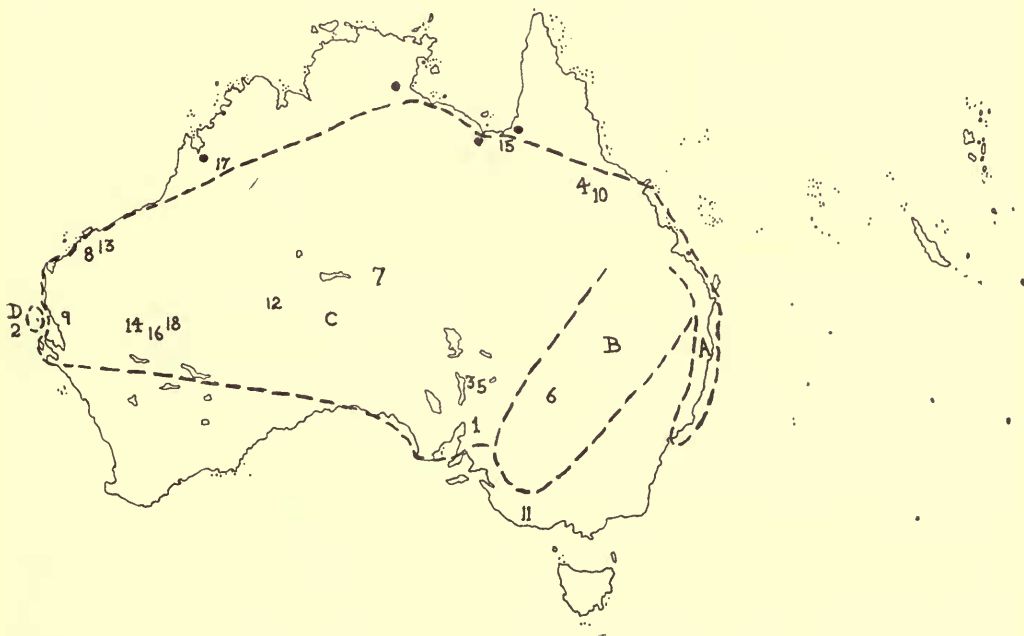
The original description of *assimilis* was based on one of the darker south-eastern specimens. Grant (1909) described *bernieri*, from Bernier Island off the west coast, differing in that the ear coverts of the male were a dark blue. In a specimen examined they are undoubtedly dark, but match well with those of a specimen from near Lake Frome in South Australia, and one from near Hughenden in northern Queensland. The third race, *mastersi* was described by Mathews (1912) from a specimen from Alexandra, Northern Territory, with more azure blue ear-coverts.

If a dark specimen is compared with a light one the difference is quite obvious, but it was found possible to lay out a series of adult males which showed a consistent gradation of forehead and ear-covert colour, from one extreme to the other, with no division at any point to suggest that more than one population was involved and there was no clear geographical pattern. The specimens, beginning with the deepest

colour, were from the following localities:—1, South Australia (unlocalized older specimen, probably from south-east settlement); 2, Bernier Island, W.A.; 3, 30 miles west of Lake Frome, S.A.; 4, near Hughenden, Qld; 5, 15 miles west of Lake Frome, S.A.; 6, Bourke, N.S.W.; 7, Finke River, N.T.; 8, Tambrey, W.A.; 9, Point Cloates, W.A.; 10, Prairie, Qld; 11, Little Desert, Vic.; 12, Warburton Mission, W.A.; 13, Tambrey, W.A.; 14, Upper Gascoyne, W.A.; 15, Moonlight Creek, Qld.; 16, Upper Gascoyne, W.A.; 17, Fitzroy River, W.A.; 18, Upper Gascoyne, W.A. (see map 2).

If one were to follow Mack (1934) nos. 6 and 11 would form his dark subspecies; no. 2 another; nos. 1, 3, 5, 7–9, 12–18 would form a pale subspecies; and nos. 4 and 10 would be part of an indeterminate population. Mack himself appeared uncertain of the precise limits of the forms which he recognized and in his map of subspecific distribution (map 2) did not show precise areas but indicated lobes from a main mass. Condon (1951), in discussing South Australian birds, abandoned head and back colour as diagnostic characters and disagreed with Mack's views on subspecific limits. Ford (1966) noted the variability of the head colouring in Western Australian birds.

There is some evidence of a general tendency for birds with deeper and darker blue colour to occur on the eastern and extreme western edges of the overall distribution, and for paler birds to be most frequent in the desert areas of Western Australia and towards the north-western limits of distribution. Perhaps Gloger's rule



MAP 2. The dotted line indicates Mack's version of the distribution of races of *M. lamberti*: A, *M. l. lamberti*; B, *M. l. assimilis*; C, *M. l. mastersi*; D, *M. l. bernieri*. The figures are those indicating individuals in the section on variation within forms. The black dots indicate the localities of variant individuals.

is involved. This clinical trend does not, however, appear to allow convenient subdivision and, in addition, there is evidence of variability between individuals in small areas as well as over a wide range. Nos. 8 and 13 from the above list were collected on the same occasion from the same party of birds, and there are similar variations within specimens from single localities at Fitzroy River, Western Australia, and in northern Queensland. T. Carter (Mathews 1922-3) noted a bird taken on the Minilya River as "blue" on the back, although most individuals from the west coast area were distinctly violet.

Other characters for separation have been suggested. Condon (1951) stated that *mastersi* could be distinguished by its clear white abdomen. This is difficult to determine in the skins of very small birds prepared by a variety of hands, but it was not apparent in the material now examined (46 males) and where some slight difference was apparent it did not relate to the earlier subspecific divisions.

Condon and others also refer to differences in the relative lightness of the brown colour of the wings. The glossy black and blue body plumage appears to be stable but the brown plumage of the wings shows a definite tendency to fade on the living bird and most of the variation apparent in specimens examined due to the differing age of the feathers, the fresh new feathers being darkest. In addition there is some change due to foxing in older specimens. The wing moult and body moult do not appear to be closely synchronised, and birds which show complete breeding plumage on the body may still be actively moulting and growing wing feathers. The relative depth of colour on the wings does not therefore provide a consistent and useful taxonomic character.

The difference in plumage between individuals within *assimilis* are so slight and gradual that there seems no reason to suppose that more than one unit is involved with some local differentiation beginning to occur. I am of the opinion that this should be treated as a single form, and *assimilis* North, 1901, is the oldest name; *mastersi* Mathews, 1919, and *bernieri* Grant, 1909, being synonyms.

MAJOR VARIATION IN THE RED-SHOULDERED WREN GROUP

Among specimens of *rogersi* a male from Kulumburu (W.A. Museum, A 8884) was a much lighter blue on the head, and similar in this respect to a specimen of *assimilis* (B.M. no. 1964. 60.585) from Moonlight Creek, north Queensland.

There is some variation in the blue tint of the head of breeding males of *amabilis*. Mack (1934) separated birds from the southern half of the range as a subspecies, *clarus*, on the grounds that they showed lighter blue colouring. An examination of specimens, including some lent by the Queensland Museum, revealed a small difference between extremes. Birds recently collected from Tully were a lighter blue than some early specimens from Somerset and Port Albany, and the latter showed a slight violaceous tint to the deeper blue which was a little more distinct on some northern birds from the Queensland Museum. Recent specimens from Ayton, towards the middle of the range of this form, appeared to be intermediate in character. The total difference appears to be small and clinal in character and on the material at present available I would regard *clarus* Mack, as a synonym of *amabilis*.

VARIANT INDIVIDUALS

In addition to the variations already described there are some variant specimens which, from their appearance and locality, (map 2) may throw some light on the relationship between various forms.

The most conspicuous of these is an adult female *assimilis* (B.M. no 1964.60.578) collected on the Norman River south of Normanton, Queensland, at the south-east corner of the Gulf of Carpentaria. This bird shows a pale greyish tint over the whole body plumage, particularly noticeable on the sides of the head and neck. The lores are the normal chestnut-red colours and the retrices dull blue. There is no suggestion that this variation is due to wear or fading. Normal brown plumage contains both eumelanin and phaeomelanin and these are not differentially affected by exposure to light, (Harrison 1963). The bird was collected from a party of eight individuals and another female and an immature male collected at the same time appear to be normal.

Two other females of *assimilis* (B.M. nos 1969.4.415, 417) show similar, although less marked, tendencies towards greyish plumage. These are the only two females taken on the Roper River, Northern Territory (14° 15'S., 135° 3' E.). On these the grey tint is superimposed on the normal brown plumage to give a colder, greyer tint, but the sides of the head and neck are noticeably grey, and the rump has an olive tint.

A minor plumage variation found during close examination was the presence of a few dark lesser covert feathers on some males of *assimilis*, the coverts of this form normally being brown. Occasional blackish covert feathers occurred on a male (B.M. no. 1964.60.674) from Norman River, at the same locality as the female described above, but from a different party of birds; and on a male (B.M. no 1964.60.585) from the south of Moonlight Creek, on the south-east of the Gulf of Carpentaria. Males showing some blue tips to feathers occurred at Moonlight Creek (B.M. no 1964.60.581), Roper River (1969.4.414, 416), and at Mount Anderson (1964.4.443, 450) in the south-western Kimberleys.

These variants may be significant in view of their distribution. The greyish females of *assimilis* occur on the edge of its range, in one case near *amabilis* and in the other near *dulcis*, both of which have blue-grey females. The variant wing-coverts similarly occur on individuals on the northern edge of the range, birds with blackish coverts at Norman River and Moonlight Creek being near *amabilis* which has similar coverts; and birds with blue covert tips at Roper River and Mount Anderson being near to *dulcis* and *rogersi* respectively, both of these having blue on the coverts. The exception is the second male from Moonlight Creek which has the few covert tips blue and not blackish.

ZOOGEOGRAPHICAL DISTRIBUTION PATTERN

The type of distribution shown by the chestnut-shouldered wren complex appears to provide a good example of the refuge concept suggested by Keast (1961) and to show the utilisation of a greater number of refuges than do the other superspecies groups which he instances. Keast did use these birds as an example but used the races as mapped (map 2) by Mack (1934) and hence found the parallels with other

species groups less obvious than they should have been. There is, in fact, a ring of forms, most of which still occupy limited peripheral areas (map 1). On the eastern edge of Australia is *lamberti*, *amabilis* is in the north-eastern peninsula, *dulcis* in the north of Northern Territory, *rogersi* in the Kimberleys of the north-west, and *elegans* in the south-west corner. Since *pulcherrimus* is present on the Eyre Peninsula as well as in the south-west it is more likely that, rather than having evolved in competition with *elegans*, it differentiated in or somewhere near the former region in a refuge demanding tolerance of drier conditions and higher temperatures than did the south-west refuge; and therefore, when conditions ameliorated, it would have been able to spread westwards into similar habitats bordering the range of *elegans*.

The last form, *assimilis*, presents a slight problem. There are several potential refuges which might have been available (Keast, 1961) and are not occupied by other members of this group, but from its present distribution it is reasonable to assume that the differentiation would have occurred in a refuge where conditions were both drier and warmer than in some others. The extreme south-east is therefore unlikely since conditions there are likely to have been both moister and cooler. The two remaining likely areas are the Hamersley region of coastal Western Australia and the central ranges. The differentiation in isolation apparent in other taxa (Keast 1961) occurs less frequently, in the latter area and the Hamersley region would seem the more likely of the two. The adaptation to such a refuge would give this form the slight advantage that would enable it to exploit more rapidly and successfully the gradual amelioration of extremely arid conditions of the central area and to spread to produce the apparent "Eyrean" distribution (Spencer 1898). Keast (1958) has pointed out that many forms with this distribution are derived from western isolates of species with more extensive distribution at an earlier period.

HABITAT PREFERENCE

From the limited distribution of some of these forms, they may have evolved some degree of habitat preference which might limit any subsequent spread. In the south-west *elegans* has a limited distribution in low cover bordering fresh water swamps or streams; while *pulcherrimus* is a species of sandplain scrub and mallee. Of the northern forms, both *rogersi* and *dulcis* occur in regions of ranges and plateaus and appear to be mainly confined to places where the floors and sides of sandstone or granite gorges have low scrubby vegetation and where natural breaks or discontinuities in the rock of the ranges are accompanied by vegetation including low bushes and spinifex. The other extreme is shown by *amabilis* which occurs on the outer edge of rain-forest or in suitable low cover in open forest adjoining it. The information on *lamberti* is poor but it appears to occupy thick, shrubby growth in fairly moist habitats including the thick shrub layer of forest, and in this respect would seem to show some similarity to *amabilis*.

As might be expected from its considerable range, *assimilis* shows a wider habitat tolerance. In general it tends to be a bird of shrubby growth bordering water-courses in drier regions. It may, however, move into the sparse vegetation of sandstone ridges, occupying a similar habitat to *rogersi* and *dulcis* in similar regions,

and although from their field observations B. M. Booth and D. Freeman are of the opinion that in such places it is less likely to venture onto bare rock than are the last two forms this would not prevent it from sharing the same cover were it to occur with them. At the other extreme it extends into the shrub growth along rivers and creeks in open forest; and down into thickets, riverine forest and the edges of mangroves.

In Western Australia near Carnarvon, where this form occurs in the scrub on dunes among saltbush, pairs were seen out in the mangroves apparently disputing territory over rising seawater. The mangroves in this area form a narrow belt separated from the beach by a tidal lagoon up to about half a mile wide in places. Within the mangroves, which are low and open on the landward side, becoming taller and thicker to seawards, there are small crescentic beaches with a sparse growth of herbaceous plants. Although it seems likely that the presence of pairs in such a place may have been due to a lack of suitable territories due to overpopulation, and the fact that these were pairs rather than parties suggests that they were young or breakaway units searching for new areas, their presence nevertheless indicates the readiness of this form to attempt to occupy a wide range of habitats.

This wide habitat tolerance in *assimilis* does suggest that the ecological requirements of the birds may be relatively simple and that, at least where the northern forms are concerned, the apparently narrower habitat preference of various other forms may be simply due to the fact that they are occupying the ecological equivalent within a more specialised and less varied biotope. Certainly the habitat tolerance of *assimilis* is such that were it to come into contact with other forms it seems likely that it would occupy the same niche, and the apparent minor variation in habitat would be unlikely to act as a barrier between them.

THE INTERACTIONS AND TAXONOMIC STATUS OF THE FORMS

Where a number of similar allopatric forms exist it is always difficult to determine their precise taxonomic relationship. In the present instance the recognition of five species for the seven forms appears to be an accidental result of the successive description of the forms and their similarity to those already known at the time of their discovery.

The situation in the south-west has been well investigated (Serventy 1951, Ford 1966, 1969). Here *elegans* and *pulcherrimus* have contiguous ranges and *pulcherrimus* and *assimilis* are sympatric in the north-west part of the former's range. Ford (1966) has evidence that these pairs encounter each other in the field; but *elegans* and *assimilis* do not meet. In such encounters these three forms appear to ignore each other and behave as good species. Where *pulcherrimus* and *assimilis* are sympatric they occur in the same biotope and show a mosaic distribution, but it is not certain whether this indicates interspecific intolerance or differing responses to microhabitats (Ford 1966).

The plumage of breeding males appears adequate to ensure specific recognition, the combination of colour on breast, head and back being conspicuously different in the three (table 1). A combination of pale azure and blue-black is present on *elegans*; violet-blue and dark violet on *pulcherrimus*; and lighter violet-blue and

black on *assimilis*. These colours would be particularly conspicuous in any frontal displays. The interspecific variation in colour of females, young and eclipse males is relatively slight, but this might aid specific recognition. There may be other differences. Ford (1966) refers to a detectable difference in the voices of *pulcherrimus* and *assimilis*. Size differences are relatively slight, with a clinal increase in a south-westerly direction; and I doubt if the differences in bill-size given by Ford would be sufficient to produce the variation in food selection which he suggests.

The situation is more complicated in the northern half of Australia where there are five recognizable forms—*lamberti*, *assimilis*, *rogersi*, *dulcis* and *amabilis*—previously recognized as three species—*lamberti/assimilis*, *rogersi/dulcis* and *amabilis*. These five forms show slight size variation of a clinal type, the more northerly being a little larger. Since within the whole chestnut-shouldered wren group size tends to increase towards the northern edge of the distributional range as well as the southern edge it seems inadvisable to suggest the latter as an example of Bergmann's rule.

Apart from this, the characters which differ between forms and could be used for recognition are those of plumage colour. In *Malurus* species generally specific and subspecific variations are usually most apparent in the breeding plumage of the male. In the present group although the dorsal blue colour varies, the range of variation within *assimilis* encompasses that of both *rogersi* and *dulcis*. In sequence from blue to violet-blue the arrangement would be *amabilis*—*lamberti*—*assimilis* (inc. *rogersi* and *dulcis*); the difference between the last two of the three, usually regarded as conspecific, being greater than that between *assimilis* and the forms in parentheses which are regarded as good species.

The only other obviously variable plumage character of breeding males, which has been used for separation of forms, is the flank colour (table 1). The posterior flanks show a variable amount of pale buff on *lamberti* and *assimilis*, slightly buff colouring on *amabilis*, and are usually white, with a purplish-grey wash on some individuals of *rogersi* and *dulcis*. One or two specimens of the last form show a small amount of pale buff, particularly around the upper thighs, but since buff is present on females and eclipse or immature males, this may only indicate incomplete assumption of full male plumage.

The female plumage shows greater distinctiveness in this group, varying between brown and blue-grey; *lamberti* being warm brown, *assimilis* normally a paler, duller brown, *rogersi* and *dulcis* pale blue-grey, and *amabilis* deep blue-grey. The apparent clear-cut distinction is blurred a little by the existence of the greyer variant individuals of *assimilis*. If these are included in the sequence there is a much smoother gradation and the most relevant differences would appear to be the darker colour of *amabilis* and the change from chestnut-red lores on *lamberti*, *assimilis* and *rogersi* to white lores on *dulcis* and *amabilis*.

The mainly allopatric distribution makes it difficult to judge the amount of interaction that might potentially occur between these northerly forms. Mack (1934) suggested that *assimilis* and *lamberti* interbred in northern Queensland, but from his account it seems possible that he did not make allowance for variation within *assimilis*, and a more satisfactory investigation of this is still needed. At the oppos-

ite extreme of the range of the latter the fifth phase of the Harold Hall Australian Expedition found both *assimilis* and *rogersi* near Mount Bell in the Leopold Range, one of the more level plain and the other in the gorges of the range, but in types of habitat in which they might well encounter each other. Intergrades between the two would be very difficult to identify. Assuming that interbreeding produced individuals with intermediate plumage colour, this would only involve the buff on the flank of the male and the body colouring of birds other than breeding males. Any male bird with buff on the flanks would probably pass as *assimilis*. Intermediates when female or immature should be recognizable and would probably resemble the greyer variant individuals of *assimilis* already described. If these single plumage characters were controlled by a simple pair of dominant and recessive alleles recognition of a hybrid might be impossible.

Rix (1970) has recently recorded a party of *assimilis* in a clump of teatree on Elsey Creek with a party of *dulcis* (referred to by Rix as *amabilis*) in an area of tall grass with a few small shrubs only about twenty yards away. There is therefore a potential zone of interaction between *assimilis* and *dulcis* also; but theoretically none between *assimilis* and *amabilis* (map 1.) However, the presence of variant individuals of *assimilis* apparently showing the plumage character of the other two to some degree, at points in its range nearest to the known ranges of the other two forms, suggests either that the factors responsible for these plumages are environmental ones which may act upon individuals of *assimilis* in the same regions and tend to select for similar characters (although in such circumstances one might expect all individuals in an area to show some evidence of this) or that there is some interbreeding within the areas where the forms approach each other. If the latter is true then it would suggest that the distribution of *amabilis* is more extensive than our present knowledge indicates. To suggest such interaction presupposes that there are not fully effective barriers of ecology or species-specific recognition between the forms. The obvious ecological barrier of habitat preference has already been discussed and it is suggested that the wide habitat tolerance of *assimilis* could potentially bring it into contact with the other forms. Recognition would be based on signals of behaviour, voice or plumage pattern. Such little evidence as we have suggests that these various forms are similar in their behaviour and that their voices are indistinguishable, although in view of Ford's (1966) comment on the voices of two south-western forms a more critical appraisal of this character might be helpful.

In the south-western forms, where plumage colour of the breeding males appears to be a good specific character, adjacent forms show marked variation in the combined colouring of head, back and breast. This suggests that such signal colouring is associated with frontal displays, and such postures have been described (Rowley 1964) in the Superb Blue Wren, *M. cyaneus*, the only adequately studied species. The present forms all have black breasts, with slight variation in the extent of the violet edge at either side. The head and back colouring is indistinguishable and variable in three forms and it is therefore difficult to argue that the slight differences in the shade of blue shown by the other two is of any great significance. The flank colour used to separate forms would not appear to be used in displays and,

in some at least, might be actually concealed by the wings. There would therefore seem to be no reason to regard the male breeding plumage as obviously specifically isolating.

An alternative isolating factor would be the recognition by the male of differences in the female colour, the grey or brown plumage, the presence or absence of chestnut-red lores, or the bill colour. Heterogynism—variation in females but not in males—occurs in races of some species but is comparatively rare. Mayr (1942) records it in three races of *Pachycephala pectoralis* in the Solomons, but since these are on different islands the question of recognition or interaction would presumably not arise. Hellmayr (1929) and Zimmer (1931 *et seq.*) also found it in races of some species of Formicariidae in South America, but the implication of this in relation to recognition does not appear to have been examined. There is therefore no useful information on the use of heterogynism in intraspecific recognition. Encounters of forms in which chestnut-red lores are present with those which lack them might produce some confusion since in the forms that possess them the absence of these usually indicates that a bird in brown or blue-grey plumage is an adult male in eclipse. Similarly a black bill on a bird in eclipse plumage usually indicates a male, but females of *amabilis* also have a black bill.

In summary, there are two very distinct forms of the chestnut-shouldered wrens in the south-west which can be regarded as separate species; but the inter-relationships of the remaining five forms are obscure. Each has a slightly different combination of plumage characters. The selection of particular characters for the previous separation of species seems to have been arbitrary, and each form would appear to represent a separate isolated evolutionary unit. The more recent taxonomic treatment of the peripheral rings of isolate forms, of which there are many in the different taxa on the Australian sub-continent, has been to regard these as species, except where secondary re-integration occurs in forms which spread and re-encounter each other, in which case they are regarded as subspecies. A typical example of the latter is Keast's (1961) interpretation of relationship in the Australian forms of *Sittella*.

In the case of the chestnut-shouldered wrens there are five distinct forms of equal standing, all of which could be regarded as specific or near-specific entities. It is possible however that speciation has been incomplete and that they might interbreed and re-integrate freely if they came together again. The extensive spread of *assimilis* has increased the likelihood that this might occur, and the existence of variant individuals suggests that it may be taking place. If subsequent field investigation shows that this is so, and if more detailed study of these forms confirms that there are no barriers, of the type discussed, to prevent this occurring, then it might be preferable to regard them as subspecies within a single species.

APPARENT EVOLUTIONARY TRENDS

The genus *Malurus* appears to have affinities with a group of genera in New Guinea (Harrison and Parker 1965, Harrison 1969a). The deep blues, black, and chestnut-red of these birds is a colour combination which appears more usually to originate in moist tropical forest; and from this, and from what we know of the

general zoogeographical trends within this region, it seems probable that *Malurus* as a unit may have invaded Australia from this direction and subsequently evolved and radiated within the Australian environment. In the New Guinea group as a whole females are similar in plumage colour to males, or as richly coloured. The production of the rather drab female plumage, and of an eclipse plumage in the non-breeding males appears to have occurred in Australia, and it would seem most likely that this is an adaptation for crypsis in a generally more open environment where the more brightly coloured bird is vulnerable to predation. In the case of the Blue-and-White Wren, *M. leucopterus*, there appears to have been a suppression of bright male plumage in subordinate males (Harrison 1969b), the alternative possibility being that of very high predation on males in breeding plumage. The species is one that occurs in arid areas with relatively sparse cover, and the blue and white male is very conspicuous.

In view of this apparent tendency to reduce the conspicuous colour of the males of this taxon in the more open areas, retention of the dull eclipse plumage on the crowns of so many of the collected male specimens of *assimilis* may be significant. With such a bird in its normal posture with tail cocked acutely and head back a little, the back is relatively less conspicuous and to an aerial avian predator the crown of the head must be the most obvious mark. A dull crown might thus carry a strong selective advantage.

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